Stock structure in western Lake Erie's yellow perch fishery: quantifying contributions from the Lake St. Clair – Detroit River corridor

Honors Research Thesis

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Introduction

Ability to quantify the relative contributions of local spawning populations (stocks) to the broader fishable population has long been a goal of marine fisheries management (Begg and Waldman 1999; Begg et al. 1999) and more recently has been recognized as a vital need in large freshwater ecosystems such as the Laurentian Great Lakes (Glover et al. 2008; Kutkuhn 1981; Sepulveda-Villet and Stepien 2011). With such knowledge of stock structure, agencies can begin to implement appropriate strategies to 1) protect important stocks that contribute disproportionately more recruits to the fishery than others, 2) rehabilitate poorly performing stocks, and 3) ensure that stock diversity is maintained. Such efforts will increase the likelihood that the fishery remains sustainable in the face of environmental change (Hilborn et al. 2003).

Identifying stock structure has historically been difficult, owing to inefficient and ineffective techniques for discriminating among individuals from different stocks and for tracking survival of their progeny to the fishery. Recent technological advances, however, have provided ways to use the genetics of individual fish (Kochzius 2009) and growth information recorded in fish otoliths (Swearer et al. 1999) as "natural" tags to address questions about stock structure (Begg and Waldman 1999; Gillanders 2009). In turn, ability to identify stock structure has improved, especially when multiple stock discrimination approaches are used simultaneously (Swearer et al. 1999; Miller et al. 2005).

The Laurentian Great Lakes support numerous economically important fish populations for which a better understanding of stock structure is needed (Kutkuhn 1981). One such example is Lake Erie's yellow perch (*Perca flavescens*) population, which supports this system's largest commercial fishery and second largest recreational fishery (Belore et al. 2011). As with yellow perch populations in other lakes (e.g., Lake Michigan; Glover et al. 2008), this need is critical in

Lake Erie because its yellow perch population is currently managed as a single stock (Belore et al. 2011), despite genetic evidence (Carreon-Martinez et al., in review; Sepulveda-Villet and Stepien 2011) and otolith microchemical evidence (Reichert et al. 2010) pointing to the existence of multiple spawning stocks within the lake.

While multiple yellow perch stocks appear to exist *within* Lake Erie proper, little is known about the relative contribution of recruits to Lake Erie's fishable population from potential external sources such as the Lake St. Clair – Detroit River corridor (SC-DRc) (Figure 1). Circumstantial evidence, however, has led me to *hypothesize* that the SC-DRc contributes larvae to Lake Erie's west basin (***Hypothesis 1***). For example, during 2006-2009, larval yellow perch were consistently captured in open waters of western Lake Erie near the Detroit River outflow at densities 5- to 10-fold greater than those associated with a south-shore stock (Ludsin et al. 2011; Reichert et al. 2010). Whether these "north-shore" larvae originated in Lake Erie or were exported from the SC-DRc remains unknown; however, the likelihood of flow-assisted transport is high as 1) high densities of larval yellow perch were found in Detroit River during 2006-2010 (Ed Roseman, USGS, Ann Arbor, MI, unpublished data) and 2) Detroit River flow rates consistently exceed the swimming speed of yellow perch larvae (Houde 1969). Further, strong positive correlations have been found between larval fish abundances in the SC-DRc and juvenile fish abundances the following year in western Lake Erie for three fishes with similar life-histories (i.e., planktonic larval stage) to yellow perch (Hatcher et al. 1991).

Despite predicted high transport of larvae from the SC-DRc into Lake Erie, I expect that the SC-DRc is not an important contributor to western Lake Erie's fishable population (i.e., SC-DRc larvae die prior to the juvenile stage; ***Hypothesis 2***). If true, then Lake Erie could be viewed as a "sink" (i.e., source of population loss) for the SC-DRc stock. My expectation is based on

research that found adult yellow perch spawners collected in the SC-DRc to be genetically distinct from Lake Erie spawning stocks (Sepulveda-Villet and Stepien 2011). Importantly, however, spawners in that study were collected at only one location in northern Lake St. Clair (Sepulveda and Stepien 2011). Thus, more investigation is warranted.

Learning whether the SC-DRc contributes larvae to western Lake Erie seems especially important to stock-structure identification efforts because recent (2006-2009) microchemical and genetics research has shown that 50 – 90% of the yellow perch that survived to the juvenile stage —which is a strong indicator of future recruitment to fishable adult population (Belore et al. 2011)—spent their larval life in waters located near the Detroit River outflow (Carreon-Martinez et al. in review; Ludsin et al. 2011; Reichert et al. 2010). Remaining recruits emanated from western Lake Eire's south-shore near the Maumee River outflow.

Herein, I explored stock structure in the western Lake Erie yellow perch population during 2006-2007. Using microsatellites in larval yellow perch as a potential natural tag, I explored whether population structure exists between the SC-DRc and Lake Erie's north and south shore stocks or if panmixia exists, perhaps owing to dispersal of SC-DRc larvae into western Lake Erie (*Hypothesis 1*). Finding significant genetic structure, I subsequently determined whether SC-DRc larvae were contributing recruits to the age-0 juvenile stage, which is a good indicator of future recruitment to the fishery at age-2 (Belore et al. 2011). Finally, to help better understand intra- and inter-annually variation in contributions of larvae from the SC-DRc, I relied on physical (e.g., Detroit River flow rates) and biological (e.g., larval growth rates, larval densities) information collected during both study years. Ultimately, I discuss the implications of these findings to fisheries management in the Great Lakes.

Methods

Study System

Lake Erie (USA-Canada) is a part of the Laurentian Great lakes system, and is highly productive across all trophic levels. Lake Erie is comprised of three distinct basins (west, central, and eastern basins) that vary in depth and productivity with a trend of average depth increasing from west to east and productivity decreasing along the same west-to-east trajectory. The west basin, which is the focus of my study, is the shallowest (mean depth = 7.4m) and most highly productive of the three basins and is an important producer of yellow perch (Belore et al. 2011; Reichert et al. 2010).

Lake Erie's west basin is an important nursery area for larvae and juveniles of many ecologically and economically important fishes, including yellow perch. Yellow perch spawning locations are largely unknown but likely many (Goodyear et al. 1982), with known larval production areas in the southern and north shores of the lake (Ludsin et al. 2001; Reichert et al. 2010). In addition, yellow perch larvae have been recently captured in the Detroit River (E. Roseman, USGS, Ann Arbor, MI), although whether they are produced there or drifted down from Lake St. Clair is unknown. Yellow perch larvae hatch at ~5 mm in total length (TL), have weak swimming abilities until ~9.5 mm TL (Houde 1969), and spend ~30-35 days in the water column feeding on zooplankton before becoming benthic as a juvenile.

Field Collections

Larvae. I used archived larval yellow perch to define genetic signatures and estimate growth rates for three local spawning populations (stocks) that could be contributing recruits to western Lake Erie's fishery. Although exact spawning locations are unknown, larvae used in this study were collected from three disparate areas during April – June 2006 and 2007: 1) the

Detroit River proper (subsequently referred to as the "DR" stock); 2) the north shore of western Lake Erie in and around the outflow of the Detroit River (the "NS" stock); and 3) the south shore of western Lake Erie in and around the outflow of the Maumee River (the "SS" stock) (Figure 1). Weekly collections of larval yellow perch were conducted from late April through June during 2006 and 2007 at up to 12 sites near the north shores (NS) and south shores (SS) of Lake Erie's western basin (Reichert et al. 2010). Larval yellow perch were collected at up to 11 sites within the southern portion of the Detroit River (DR) during May to early June in 2006 and2007 (E. Roseman, USGS, Ann Arbor, MI, unpublished data). All larval yellow perch were collected with paired (1-m diameter) bongo nets towed ~1 m from the bottom of the lake to the surface (500-µm mesh). All larvae were preserved in 100% ethanol until identification and were transferred to 95% ethanol for storage until the experiment.

Juveniles. Juvenile yellow perch were collected during late August in both 2006 and 2007 (n= ~70 sites per year) via bottom trawling (10 - m head rope; 3 km/h tow speed) conducted by the Ohio Department of Natural Resources and the Ontario Ministry of Natural Resources as part of annual assessment surveys across the entire western basin (Reichert et al. 2010). For the genetic analyses of this study, 119 (in 2006) and 167 (in 2007) juveniles were used with individuals randomly chosen from trawls based on trawl-catch proportions. These individuals were stored frozen until processing (Reichert et al. 2010).

Molecular Approach

Procedures for DNA extraction and genotyping for all individuals followed the methods of Carreon-Martinez et al. (in review), with DNA from tissue samples extracted using plate-based extraction (Elphinestone et al. 2003). A 50-µL Tris-EDTA buffer (10 mM Tris, 1.0 mM EDTA, pH 8.0) was used for larval samples, while 100 µL of the buffer was used for juvenile

samples. Nine loci were genotyped per individual and PCR amplification involved 25-µL reactions with 1.5 µL of template DNA, 2.5 µL of a 10x PCR buffer, 2.5 µL of $MgCl_2$ (25mM), 0.3 µL of dNTPs (50 µM of each), 0.2 µL (0.5µM) of a dye-labeled primer, 0.2 µL (0.5 µM) of the reverse primer, and 0.10 U Taq polymerase (Carreon-Martinez et al. in review). PCR conditions included initial denaturation at 94ºC for 2 min, followed by 35 to 40 cycles of denaturing at 94ºC for 15 s, annealing for 30 s, extension at 72ºC for 30s, and a final extension at 72ºC for 10 min (Carreon-Martinez et al. in review). Microsatellite allele sizes were determined using a LI-COR 4300 DNA analyzer and scored using GeneImage IR 4.05 (Carreon-Martinez et al., in review). In total, I processed 297 larvae captured in 2006 (n = 53 from DR, n = 154 from NS, n = 90 from SS) and 427 larvae captured in 2007 (n = 64 from DR, n = 282 from NS, n = 81 from SS) (Table 1).

Statistical Analysis

Population genetic structure. I used multiple approaches to explore the degree of genetic structure among DR, NS, and SS larvae (i.e., to test *Hypothesis 1*). First, I performed exact tests for Hardy-Weinberg Equilibrium (H-Weq) using Tools for Population Genetic Analysis (v1.3; Raymond and Rousset 1995; Miller 1997). Because each locus can be viewed as an independent assessment of whether a population meets H-Weq assumptions, I adjusted the α-level of each test by dividing by the number of tests conducted (i.e., nine tests, one per locus). In so doing, I could preserve the desired family-wise Type I error rate of 5%. In addition, this test was used to help determine if any the loci were unreliable, as would be indicated by consistent violations of H-Weq by the same locus across all three stocks. Second, I calculated F_{ST} estimates to assess genetic differentiation among DR, NS, and SS stocks using Genepop (version 4.0.7; Rousset 2008, following Weir and Cockerham 1984). Third, I used pairwise Fisher exact tests (10,000

dememorizations and 20, 000 permutations), using Tools for Population Genetic Analysis (v1.3; Miller 1997; Raymond and Rousset 1995), to explore whether allele frequency distributions varied among the three stocks. Doing so provided another assessment of genetic structure that is not dependent on H-Weq assumptions. Finally, I used an analysis of molecular variance (AMOVA; Excoffier et al. 2005; following Weir and Cockerham 1984) test to explore inter-annual variation in genetic structure, including whether it superseded within-year variation in stock structure. Unless otherwise noted, p-values < 0.05 were considered statistically significant.

Assignment accuracy. I used a rank-based self-assignment genotype test (Carreon-Martinez et al. in review, Paetku et al. 1995), which was based on the microsatellite data in GENECLASS 2.0 (Carreon-Martinez et al. in review, Piry et al. 2004) from larvae from all three stocks, for two purposes. First, I used it to assess the accuracy of stock-specific genetic signatures for potentially typing back juvenile yellow perch of unknown origin. This test uses a bootstrapping approach wherein each individual larva is removed from the analysis (one at a time) and subsequently treated as an "unknown" larva that is then assigned to 1 of the 3 stocks, based on the genetics of all other individuals (Paetku et al. 1995). By determining the percent of larvae correctly assigned back to their collection site, as well as exploring posterior probabilities of assignment for each individual, I could assess reliability in assignments for each stock. Second, I used this analysis to better understand the genetic relatedness of the three stocks. To do so, I used misclassified fish to determine which stocks were being misclassified as another. My expectation was that the DR stock would be misclassified as the NS stock (or vice versa) more often than the DR stock and the SS stock, owing to the close geographical proximity of the DR and NS stocks.

Juvenile assignments. I used a two-step process to assign juveniles of unknown origin to a larval production site (test *Hypothesis 2*), following the methods of Beneteau et al. (2009). In the first step, a Bayesian assignment was conducted (Rannala and Mountain 1997) with Monte Carlo re-sampling, using a simulation algorithm (10,000 simulated individuals at an assignment threshold $p = 0.05$; Paetkau et al. 2004). Following Bayesian assignment, I removed from the analysis juveniles that were unlikely to have originated from any of the three larval source populations being explored herein. Such a possibility exists, given that larvae have a long, passive pelagic larval stage that can make them susceptible to stochastic, wind-driven circulation (Beletsky et al. 2007; Houde 1969), not to mention that juveniles can potentially move actively between lake basins. For this analysis, I removed juveniles with a probability of assignment to any one of the three subpopulations that was less than 0.3 (Carreon-Martinez et al. in review; Rannala and Mountain 1997). In the second-step, each remaining juvenile was assigned to the DR, NS, or SS as its natal site with an individual-based posterior probability of assignment. Only individuals with a posterior probability of assignment ≥ 0.70 were considered reliable.

Age and Growth-Rate Estimation

I used otoliths to estimate the hatch date, age at capture, and daily growth rate (Campana 1999) of larvae. Methods for otolith extraction and age and growth rate analysis followed those of Reichert et al. (2010). Briefly, I extracted and analyzed sagittal otoliths from larvae collected in the Detroit River during 2006 and 2007 ($n = 30$ random individuals per year). Utilizing NIS Elements imaging software and a Nikon E200 compound microscope (100x and 50x magnification, oil immersion), I counted post-hatch daily rings and measured the total otolith radius (core to otolith edge), hatch radius (hatch check to otolith edge), and daily growth increments of each otolith. These collections supplemented archived data from NS and SS

yellow perch larvae (Table 1), which were previously analyzed for a different purpose but following the same methods (Ludsin et al. 2011; Reichert et al. 2010). For all stocks, otolith ages from fish less than 25 d old were determined from a single count as previous research conducted with Lake Erie yellow perch (Ludsin et al. 2001) has shown that single ring counts are reliable for yellow perch less than this age (Table 1). For larvae > 25 d of age, at least one additional blind count was conducted, with additional counts being performed as needed (see Reichert et al. 2010 for details).

I used otolith daily increment counts and width measurements for several purposes. Ring count information was used to estimate the hatch date for each individual, which helped me assess whether fish collected in each region were the same age. Because stock- and growth-dependent survival of larvae has been documented in western Lake Erie (Carreon-Martinez et al. in review; Ludsin et al. 2011; Reichert et al. 2010), I wanted to ensure that no bias was induced in understanding larval recruitment patterns to the juvenile stage because of age-at-collection differences among stocks. Otolith increment widths were used as a proxy for mean somatic growth rate (μm/day) during the first 10 d of life for each individual, as previous research in western Lake Erie has demonstrated strong, positive relationships between larval yellow perch total length (TL) and total otolith radius across a wide range of years (Ludsin et al. 2001, Reichert et al. 2010). I then tested for growth-rate differences among DR, NS, and SS larvae during the first 10 d of life using Kruskal-Wallis tests (owing to heterogeneous variances) with 2-tailed post-hoc comparisons, as well as Kolmogorov-Smirnov two-sample tests, which could potentially help understand any found stock-specific differences in recruitment to the juvenile stage (both within and between years). The α-level for these Kolmogorov-Smirnov tests was adjusted for each year to 0.0167, to account for 3 pairwise tests conducted within each year.

Detroit River Flow and Larval Export

To potentially help understand the role of Detroit River larval production and flow rate to patterns in recruitment of larvae from the DR stock to the juvenile stage, I estimated total larval export from the Detroit River for both 2006 and 2007. To do so, I multiplied daily Detroit River discharge rates (m^3/s; U.S. Army Corps of Engineers, unpublished data) with mean larval yellow perch densities (# individuals/m^3) in the Detroit River on each sampling each day. I used linear interpolation to estimate yellow perch densities between weekly sampling dates. Afterwards, I converted my export estimate (# of individuals/s) to daily export (assuming equal transport of larvae throughout the entire day) and summed the daily export over the collection seasons for each year (5 May – 15 June during 2006; May – 20 June 2007). This export was compared to estimated in-lake production of larvae from both the NS and SS stocks, which essentially consisted of multiplying peak larval yellow perch density in a year in both the NS and SS by half the total west basin area and mean west basin depth (Ludsin et al. 2011; Reichert et al. 2010;). Using these estimates of total stock-specific production, I determined expected contributions of larvae from each stock to the juvenile stage (sensu Reichert et al. 2010).

Results

Genetic Structure

Pairwise F_{ST} values, based on the nine loci evaluated (diploid), indicated a high degree of genetic differentiation among stocks in both years (Table 2). During 2006, F_{ST} values ranged between 0.002 and 0.0165 with each population differing significantly from the other, based on Bonferroni-adjusted Fisher exact tests. F_{ST} values were greatest between the geographically most disparate stocks (DR and SS) followed by the DR and NS and then finally both Lake Erie

stocks (NS and SS). Near identical results were evident during 2007, with the exception that genetic differentiation between stocks was greater than during 2006 (Table 2).

We calculated exact p-values, using the Markov chain method (Genepop version 4.0.7), to assess deviations from H-Weq at each individual locus. After Bonferroni-correcting our significance level for nine simultaneous tests, p-values < 0.0056 were considered to significantly deviate from H-Weq. For 2006, 4, 3, and 2 of the 9 loci deviated significantly from H-Weq for larvae from the DR, NS, and SS, respectively. Importantly, however, no single locus deviated significantly from H-Weq across all three populations during 2006 (Table 3). For 2007, 1, 4, and 5 of the 9 loci deviated significantly from H-Weq for larvae from the DR, NS, and SS, respectively. Again, no single locus deviated significantly from H-Weq across all three populations for the year 2007 (Table 3).

Fisher's exact G tests (Genepop version 4.0.7) were used to compare allele frequency distributions (from the nine loci) between the stocks for 2006 and 2007. Following a Bonferroni-correction for multiple simultaneous comparisons (n = 3), p-values < 0.017 were considered significant. Results of these tests support the F_{ST} results, which may be biased, owing to violation of H-Weq conditions. Allele frequency distributions differed between the DR and NS stocks, as well as between the DR and SS stocks, during both 2006 and 2007 (both were highly significant, $p<0.001$, df = 18). Allele frequencies also differed between the NS and SS stocks during 2006 ($p = 0.001$, df =18), although no significant difference was detected between these stocks during 2007 ($p = 0.035$, df = 18) (Table 2).

An AMOVA used to identify the sources of variation between years (2006 and 2007), among populations (DR, NS, and SS stocks) within years, and within populations demonstrated that differences in genetic structure between years explained little (0.00%) of the overall

variation. By contrast, differences among stocks within years explained a higher fraction (0.44%) of the variation with the remaining 99.58% of the variation being due to a high degree of variation among individuals within populations.

Assignment tests

Larval self-assignment. During 2006, the DR and SS stocks demonstrated a decent ability to correctly classify individuals captured at these sites, with correct classification accuracies of 68% (DR) to 72% (SS), respectively. Larvae collected in the Detroit River were misclassified as the geographically closer NS stock (n = 19) more often than the more distant SS stock (n = 13) during 2006 (Table 4). Likewise, misclassified larvae from the SS stock were assigned to the geographically closer NS stock (n = 20) than the more distant DR stock. Assignment accuracy for the NS stock was the lowest at 52%, with misclassified larvae being confused more with the SS stock (n = 36) than DR stock (n =12) (Table 4).

During 2007, near-identical results were produced with the DR and SS stocks showing the highest classification accuracies of 80% (DR) and 68% (SS). Larvae collected in the Detroit River were misclassified more often as the NS stock (n = 7) than as the SS stock (n =6) and larvae collected in the SS were more often misclassified as the NS stock (n =17) than as the more geographically distant DR stock (n = 9). Larvae collected in the NS had a 49% classification accuracy, with these larvae being misclassified as SS fish (n = 85) more often than DR fish (n = 59) (Table 5).

Juvenile assignment. A total of 286 juveniles collected in the western basin of Lake Erie were genotyped at the same nine microsatellite loci as the larvae. During 2006 and 2007, 3 (of 119) and 37 (of 167) individuals were eliminated from analysis, respectively, owing to a Bayesian probability of assignment < 0.3 (i.e., these individuals had less than a 30% chance of

originating from 1 of the 3 stocks; Carreon-Martinez et al. in review; Rannala and Mountain 1997). For remaining individuals that were classified to a source stock (DR, NS, or SS), those with a posterior probability of assignment of < 0.70 were considered failed assignments. This second cutoff removed 98 and 109 of the juveniles from the analysis during 2006 and 2007, respectively (Table 6). This cutoff was used, as it approximates the minimum self-assignment accuracy of the DR larvae during both years (Tables 4 and 5). Of the remaining 18 larvae classified during 2006, 17%, 50%, and 33% of them were typed back to the DR, NS, and SS, respectively (Table 7). During 2007, the 21 juveniles were assigned to all three source stocks, with the largest fraction of juveniles (52%) being assigned to the DR stock. Assignment to the NS and SS stocks was equal during 2007 (24% each) (Table 6).

If the posterior probability cutoff was raised from 0.70 to a more stringent 0.80 minimum assignment accuracy threshold, only 6 and 9 fish could be assigned successfully to a natal stock in 2006 and 2007, respectively. Of these, 5 and 1 individuals assigned to the NS and SS, respectively, in 2006 and 6 and 3 individuals assigned to DR and NS, respectively, in 2007.

Larval Growth Rates

Larvae used to quantify mean growth rate during the first 10 d of life in the DR, NS, and SS stocks were of the same approximate age, length, and spawning cohort (see Table 1). However, the mean growth rate of larvae significantly differed among stocks during both 2006 (Kruskal-Wallis test: $H_{2,90} = 53.7$, $p < 0.0001$) and 2007 (Kruskal-Wallis test: $H_{2,99} = 60.6$, $p < 0.0001$). Based on Kruskal-Wallis post-hoc multiple comparisons, mean growth rates were significantly lower in the DR stock (mean ± SD = 1.1 ± 0.3 µm/day in 2006; 1.3 ± 0.3 µm/day in 2007) than in the NS (mean ± SD = 2.3 ± 0.5 µm/day for NS in 2006; 2.0 ± 0.3 µm/day for NS in 2007) and SS (mean ± SD = 2.3 ± 0.5 µm/day for NS in 2007; 2.5 ± 0.3 µm/day for SS in 2007)

stocks during both years. During 2006, no significant difference in average daily growth rate was found between the NS and SS stocks; however, larvae from the NS stock grew slower during their first 10 d of life than SS larvae in 2007. Kolmogorov-Smirnov two-sample tests also revealed significant differences between cumulative frequency distributions of average daily growth rate during the first 10 d of life for the DR stock and both Lake Erie stocks during both years (all $p < 0.0167$); in both years, the cumulative frequency distribution for the DR stock was shifted to left, indicating significantly lower daily growth rates (Figure 2). Cumulative frequency distributions of larval growth rate did not differ between the NS and SS stocks during either year (both $p > 0.0167$; Figure 2).

Discussion

Genetic Structure

My suite of findings demonstrates that significant genetic structure exists for yellow perch residing in the St. Clair-Detroit River corridor (SC-DRc) and western Lake Erie. Fisher's exact tests showed that larvae captured in the lower Detroit River proper (DR stock) had allele frequency distributions completely different from larvae originating in western Lake Erie's north shore (NS) or south shore (NS) during both 2006 and 2007. Likewise, differences in allele frequency distributions were evident between NS and SS larvae during 2006 (but not 2007), although this difference was not as great as found between the DR and either Lake Erie stock. Further, when using larvae to create characteristic signatures for their collection location (DR, NS, and SS), I found—during both 2006 and 2007—strong evidence to suggest that some of the age-0 juvenile yellow perch captured in western Lake Erie during August assigned back to the

DR. Thus, population connectivity appears to exist between the SC-DRc and Lake Erie, with the Detroit River clearly contributing larvae (and even some juveniles) to Lake Erie's western basin.

Because of my results regarding the genetic structure of yellow perch in Lake Erie, microsatellite analysis appears to be an effective technique in discerning local spawning stocks at small spatial scales. Other Great Lakes research has drawn a similar conclusion. For example, using adult fish captured during the spawning season, Stepien et al. (2009) showed that yellow perch spawning stocks could be discriminated with high confidence between Lake Erie and Lake St. Clair. Similar to our findings, Stepien et al. (2009) showed that discerning between stocks within Lake Erie proper was more difficult. While the reason for poor stock discrimination within Lake Erie is unknown, it may arise from interbreeding between stocks, owing to adult spawners "straying" from their natal spawning location (e.g., Fraser et al. 2007).

Another possibility, which is more relevant to our study, is that reduced discrimination between stocks arises from imperfect sampling, owing to river flow or wind-driven circulation that transports larvae from their natal location into the natal location of another stock prior to collection for development of a site-specific genetic signature. In this way, the suite of larvae I used to characterize the NS, for example, might actually have consisted of a mix of larvae mostly produced locally and a lesser number of individuals that were physically transported there from another location (e.g., DR or SS). Indeed, geographically close stocks in my study were less genetically distinct than those far apart. Specifically, the DR and SS stocks were more differentiated than were the DR and NS or NS and SS during both 2006 and 2007. While simulations have not been run for my study years, a Lake Erie hydrodynamic simulation from 2011 has shown that Detroit River yellow perch larvae with a simulated release location and hatch date that is identical to where my DR larvae were collected for this study were transported

into both NS and SS areas within 2d after hatch (K. DeVanna and S. Ludsin, The Ohio State University, Columbus, Y. Zhao, Ontario Ministry of Natural Resources, Wheatley, ON, and E. Roseman, USGS, Ann Arbor, MI). Similar long-distance transport of larvae via river flow and wind-driven circulation has been documented both in the Great Lakes (Beletsky et al. 2007; Hook et al. 2006; Mion et al. 1998) and marine ecosystems (Cowen et al. 2003; Hogan et al. 2012).

While the F_{ST} values calculated for DR and Lake Erie (NS, SS) yellow perch population pairs in our study (0.0129 – 0.0251) can be considered low relative to some populations (e.g., landlocked Atlantic salmon *Salmo salar* in Lac-Saint Jean, Canada, F_{ST} = 0.109; Fraser et al. 2007), they are certainly within the range of values for other species that exhibit homing with some degree of straying (e.g., brown trout *S. trutta*; F_{ST} = 0.018 to 0.063; Carlsson et al. 1999; Fraser et al. 2007). Further, these values are high when compared to the average F_{ST} value (0.005) found among populations of adult fish within coral reef systems in Mexico known to exhibit high dispersal rates (Hogan et al. 2012). Our F_{ST} values for NS-SS population pairs (~0.002), however, were closer to the range of F_{ST} values for coral reef systems with high rates of larval dispersal.

Population Connectivity

While the genetic structure found between the Detroit River and Lake Erie in our study is consistent with Stepien et al.'s (2009) findings for Lake St. Clair and Lake Erie, we disagree with their implied suggestion that these two systems are not connected. Two lines of evidence exist to support our contention that these populations are connected. First, circumstantial evidence supports this conclusion in that our larvae were collected in the lower reaches of the Detroit River at a time when flow rates exceeded, 0.032 m/s, which is the sustained swimming

speed of larvae (i.e., 10 mm total length) used in this study (Houde 1969). Indeed, previous research has suggested larvae from other fishes are transported from the Detroit River into western Lake Erie (Hatcher et al. 1991). Second, our juvenile assignments lend strong support to this notion as a small proportion of juveniles captured in Lake Erie during 2006 and 2007 typed back with high confidence to the Detroit River. Even when I implemented a more rigorous cutoff for posterior probability of assignment of 90%, three juveniles assigned back to the DR in 2007 (Figure 3).

Maintenance of Genetic Structure

I propose three mechanisms that can explain how genetic structure can be maintained between the DR and western Lake Erie stocks in the face of connected populations via larval dispersal. First, homing behavior to natal spawning sites may exist for SC-DRc yellow perch despite the mixing of individuals during early life stages. Indeed, such homing behavior has been demonstrated in other fishes, both freshwater (Kapuscinski et al. 2005; Neville et al. 2006; Stepien et al. 2009) and marine (Ruzzante et al. 2006; Walther et al. 2008). Second, although remote, the possibility exists that DR fish transported into Lake Erie remain there in small numbers (perhaps in a different lake basin) and do not interbreed with adults from NS or SS larvae. Such reproductive isolation among sympatric subpopulations may arise via kin selection, as has been found in Lake Constance, Germany for European Perch (*Perca fluviatilis*), a congener of yellow perch (Gerlach et al. 2001), as well as a variety of other fishes (Piyapong et al. 2011; Sikkel and Fuller 2010). Perhaps, however, this mechanism can help explain how genetic variation is maintained between NS and SS stocks in western Lake Erie (Carreon-Martinez et al. in review). Third, growth-dependent survival offers another possible mechanism to explain the maintenance of genetic differentiation between the DR and NS/SS stocks.

Ludsin et al. (2011) and Carreon-Martinez (2012) provide a wealth of evidence to demonstrate that both predation risk and mortality were higher in Lake Erie's north shore than south shore during my study years (2006-2007), owing to formation of the turbid, open-lake Maumee River plume in the south shore during the larval yellow perch production period that provided a predation refuge for larvae. In turn, larvae that resided in this south-shore plume recruited disproportionately better to the juvenile stage than those living outside of it during both years (using genetics and otolith microchemistry and as natural tags; Carreon-Martinez et al. in review; Ludsin et al. 2011; Reichert et al. 2010). Further, in both areas of the west basin, individuals that survived to the juvenile stage during 2006-2007 grew faster during their first two weeks of life than those that did not, with selection against slow growth being more evident in the north shore than south-shore Maumee River plume (Ludsin et al. 2011). The fact that larvae from the DR stock 1) grew even slower than both NS and SS larvae, 2) were more likely retained in the Detroit River plume in the north shore rather than being advected into the south-shore Maumee River plume where turbidity could provide a refuge from predators, and 3) were entering Lake Erie in relatively small numbers (as compared to the estimated number of larvae found in Lake Erie proper during spring; Table 7), I find it highly probable that the larvae transported into Lake Erie die of natural causes (e.g., predation) either as larvae or juveniles before they reach a length threshold that reduces predation risk or perhaps as an adult due to recreational or commercial fishing.

Study Limitations

While I did find that microsatellite analysis coupled with otolith growth rate analysis was effective in discerning yellow perch population structure in the SC-DRc-Lake Erie subsystem of

the Great Lakes, my study has some apparent limitations. For one, I had several microsatellite loci that violated H-Weq, though no single locus violated these assumptions across all populations (indicating that this violation of assumptions did not stem from inappropriate microsatellite selection). These violations of H-Weq seem to point at a biological explanation. Or, perhaps the use of larvae is responsible as larvae undergo a lot of mortality (i.e., populations are not stable, which is assumed by H-Weq), and hence, they may not represent the genetics of the spawners.

Despite apparent violations of H-Weq, the suite of other results that are not dependent on these assumptions (e.g., Fisher exact tests, AMOVA results, juvenile assignments) still point to strong genetic structure that support my F_{ST} findings. Even so, I encourage future research that explores population connectivity and genetic structure in this ecosystem using a comparative genetics approach, wherein the same questions asked herein are addressed using larvae and adult spawners. Such an approach would help identify the robustness of our results to violations of the assumptions of H-Weq, as well as identify how the selection of life stage can influence assessments of genetic structure and population connectivity.

Conclusions and Recommendations

My study has several clear implications for yellow perch fishery management. First, my study found strong evidence for the contribution of a novel stock (DR stock) to the western basin of Lake Erie, with evidence of survival of some larvae to the juvenile stage. While the contribution of this DR stock was low relative to stocks in Lake Erie proper, perhaps its contributions are higher in other years of high flow or larval production. Toward this end, I found higher recruitment of DR larvae to the juvenile stage in western Lake Erie during 2007 relative to 2006 (Table 7). Given 1) near identical flow rates during spring in the Detroit River

during 2006 and 2007 (5,093 m^3s^{-1} and 4,981 m^3s^{-1}, respectively, U.S. Army Corps of Engineers, unpublished data) and 2) ~20% higher densities of larval yellow perch in the Detroit River in 2007 as compared to 2006 (Ed Roseman, collaborator, USGS, Ann Arbor, unpublished data), I attribute larval production (i.e., propagule pressure) to the greater juvenile contributions in 2007 rather than greater Detroit River flow rates. If true, then perhaps the DR could become a larger contributor of larvae to western Lake Erie's yellow perch population, if fish habitat rehabilitation efforts continue in the SC-DRc.

I recommend use of hydrodynamics models in studies such as this one, which involve potential connectivity via passive larval dispersal. Hydrodynamics modeling in conjunction with genetic analyses could assist in evaluating annual contributions of larvae from a donor population (e.g., SC-DRc) to its recipient population (Lake Erie) and also in beginning to describe the low classification accuracies in larval self-assignment tests. Hydrodynamics models specific to the western basin of Lake Erie and its two primary tributaries (i.e., the Detroit and Maumee rivers) could quantify the likelihood that larvae actually originate in the sites in which they are captured.

I encourage continued research that is focused on quantifying contributions of the SC-DRc to the western basin yellow perch population, as this stock may have been important historically (during periods of high flow) or may become more important with changing climatic conditions and nutrient regimes or continued rehabilitation efforts in the SC-DRc. Additionally, I support future research aimed at identifying whether yellow perch are actually spawning in the Detroit River, or if they might have originated upstream in Lake St. Clair. Such knowledge could help target habitat rehabilitation efforts in support of boosting stock production. Or, perhaps the larvae that are captured in the Detroit River are weak swimmers with slow growth

rates that are advected from Lake St. Clair during high St. Clair River flows. Such a finding might help to understand the low growth rates of DR larvae relative to NS and SS individuals and would suggest that Lake Erie simply may represent a sink for poor-performing St. Clair larvae that do not warrant protection.

My research also suggests that a single-stock and single-system approach to management, which is currently used in Lake Erie (Belore et al. 2011), is inadequate given the clear connectivity between the Detroit River corridor and western Lake Erie through larval exchange. Because the Detroit River and Lake Erie are bi-nationally managed systems, this connectivity between Lake Erie and the Detroit River highlights the need for continued bi-national collaboration in terms of both management and research. Certainly, continued integrative efforts to 1) understand stock structure with in this Great Lakes subsystem and 2) further discern and quantify contributions via the Detroit River in years with varying flow rates or larval production rates will begin to allow for development a reliable multi-stock approach for managing this economically and ecologically important fishery into the future.

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Table 1. Characteristics of yellow perch larvae used to explore population structure in the Detroit River (DR), north-shore western Lake Erie (NS), and south-shore western Lake Erie (SS) stocks during 2006 and 2007. Mean (± 1 standard deviation) hatch date (day of year), age at capture (d), and total length (TL; mm) are provided, as are the minimum and maximum values for each attribute (in parentheses).

	2006			**2007**		
	DR	NS	SS	DR	NS	SS
Hatch day	126.19±3.96 (112-134)	131±5.86 (113-138)	122±4.23 (113-134)	127±5.73 (116-140)	131±4.10 (121-137)	127±3.63 (120-139)
Age	6±4.96 (1-25)	16±9.71 (2-32)	13±7.59 (4-30)	9±3.82 (3-19)	14±6.96 (4-30)	11±3.32 (4-17)
TL	8.2±1.46 (4-11)	8.5±2.31 (5.90-16.74)	8.2±1.78 (6.39-13.02)	7.7±0.50 (6.7-8.6)	8.3±1.97 (5.58-12.15)	7.40±0.44 (6.14-7.99)

Table 2. Pairwise F_{ST} values for yellow perch larvae collected in the Detroit River (DR) and north shore (NS) and south shore (SS) of western Lake Erie during 2006 (06) and 2007 (07). Asterisks denote significance, using Fisher exact tests (not reported here) with a Bonferroni-corrected α level = 0.0167 due to three comparisons per year.

Year		**2006**	
	Stock	**DR**	**NS**
2006	**NS**	0.0129*	
	SS	0.0165*	0.0020*
		2007	
		DR	**NS**
2007	**NS**	0.0167*	
	SS	0.0251*	0.0022

Table 3. Exact test results for Hardy-Weinberg Equilibrium (H-Weq) for larval yellow perch in the western basin of Lake Erie. Individual p-values are given by locus, collection site (Detroit River, North Shore, South Shore), and year (2006, 2007). After Bonferroni correction for multiple tests (n = 9), p-values less than 0.0056 (shaded) indicate loci that deviated significantly from H-Weq.

	Detroit River		**North Shore**		**South Shore**	
	2006	**2007**	**2006**	**2007**	**2006**	**2007**
Locus			**P-value**			
85	0.0000	0.0211	0.1425	0.0393	0.0000	0.0000
78	0.0203	0.0408	0.0000	0.0000	0.0024	0.0000
41	0.0000	0.0001	0.0224	0.5412	0.0092	0.8030
55	0.0000	0.0928	0.9940	0.0226	0.0107	0.0383
110	0.0053	1.0000	0.3446	0.5967	0.0129	0.2928
96	0.0538	0.1110	0.0036	0.0000	0.0830	0.0004
60	0.0602	0.2865	0.2624	0.0000	0.0079	0.0000
49	0.0103	0.0237	0.0000	0.0000	0.5415	0.0000
99	0.1114	0.1261	0.0488	0.0958	0.0261	0.1625
#violate (n)	4	1	3	4	2	5

Table 4. Larval yellow perch larval self-assignment results for 2006. Larvae were collected in the north (NS) and south (SS) shores of the western basin of Lake Erie, as well as the Detroit River (DR). Numbers indicate the percentage of individuals assigned to each respective stock-pair.

		Assigned as		
		DR	**NS**	**SS**
Collection Site	**DR**	68	19	13
	NS	12	52	36
	SS	8	20	72

Table 5. Larval yellow perch larval self-assignment results for 2007. Larvae were collected in the north (NS) and south (SS) shores of the western basin of Lake Erie, as well as the Detroit River (DR). Numbers indicate the percentage of individuals assigned to each respective stock-pair.

		Assigned as		
		DR	**North**	**South**
Collection Site	**DR**	80	11	9
	North	21	49	30
	South	11	21	68

Table 6. Age-0 juvenile yellow perch assignment results following Bayesian correction (<30% likelihood of originating from any of the three larval populations were 'Excluded'). Juveniles with probabilities of assignment between 30% and 70% were considered "Failed" and those with a probability $\geq$ 70% were assigned to their respective larval populations (DR , NS, SS). Larvae used to assign juveniles were collected in the north (NS) and south (SS) shores of the western basin of Lake Erie, as well as the Detroit River (DR).

	Juvenile Assignment					
	DR	**NS**	**SS**	**Failed**	**Excluded**	**Total**
2006	3	9	6	98	3	119
2007	11	5	5	109	37	167

Table 7. Estimated export of larval yellow perch production from the Detroit River (DR) and estimated production of larval yellow perch in the western basin of Lake Erie during 2006 and 2007. Percent contribution to the juvenile life stage expected and observed from the DR based on larval production estimates between sites for each year. Observed percent contributions were based on genetic assignment results for juvenile yellow perch captured in Lake Erie's western basin (excluding "Exclude" or "Failed" juveniles per Table 6).

	2006	**2007**
DR exported production	9.83E+08	1.23E+09
Lake Erie production	7.49E+10	9.54E+10
% Contribution *expected* from DR	1.3%	1.3%
% Contribution *observed* from DR	16.7%	52.4%

Figure 1.

Figure 1. Great Lakes map (left). Lake Erie's western basin and the Lake St. Clair-Detroit River corridor (SC-DRc) (right). Ovals indicate sampling locations for yellow perch larvae in 1) Lake Erie's south shore (n = 12 sites), 2) Lake Erie's north shore (n = 12 sites), and 3) the Detroit River proper (n = 11 sites) during 2006 and 2007.

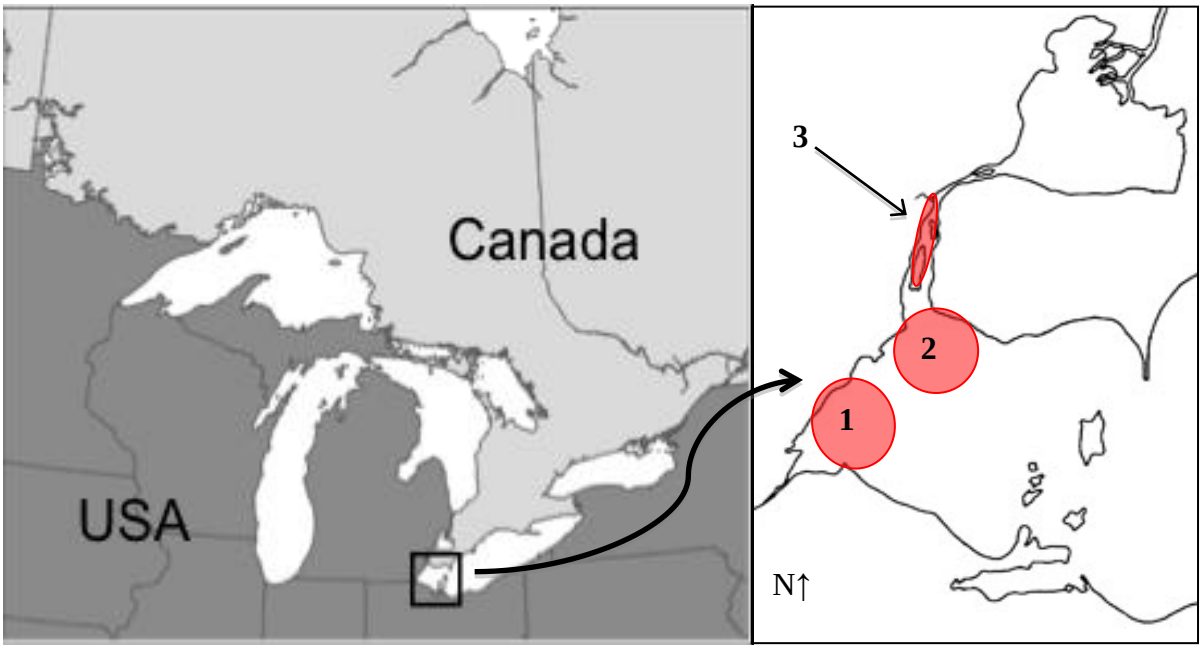

Figure 2. Cumulative frequency distributions of otolith growth rates (µm/d) for Detroit River (DR), Lake Erie north shore (NS), and Lake Erie south shore (SS) larval yellow perch. Growth rates were averaged during the first 10 d of life in larvae less than 19 d old. Solid lines are 2006 stocks and dotted ones 2007 stocks. Green, red, and blue lines correspond to DR, NS and SS stocks, respectively.

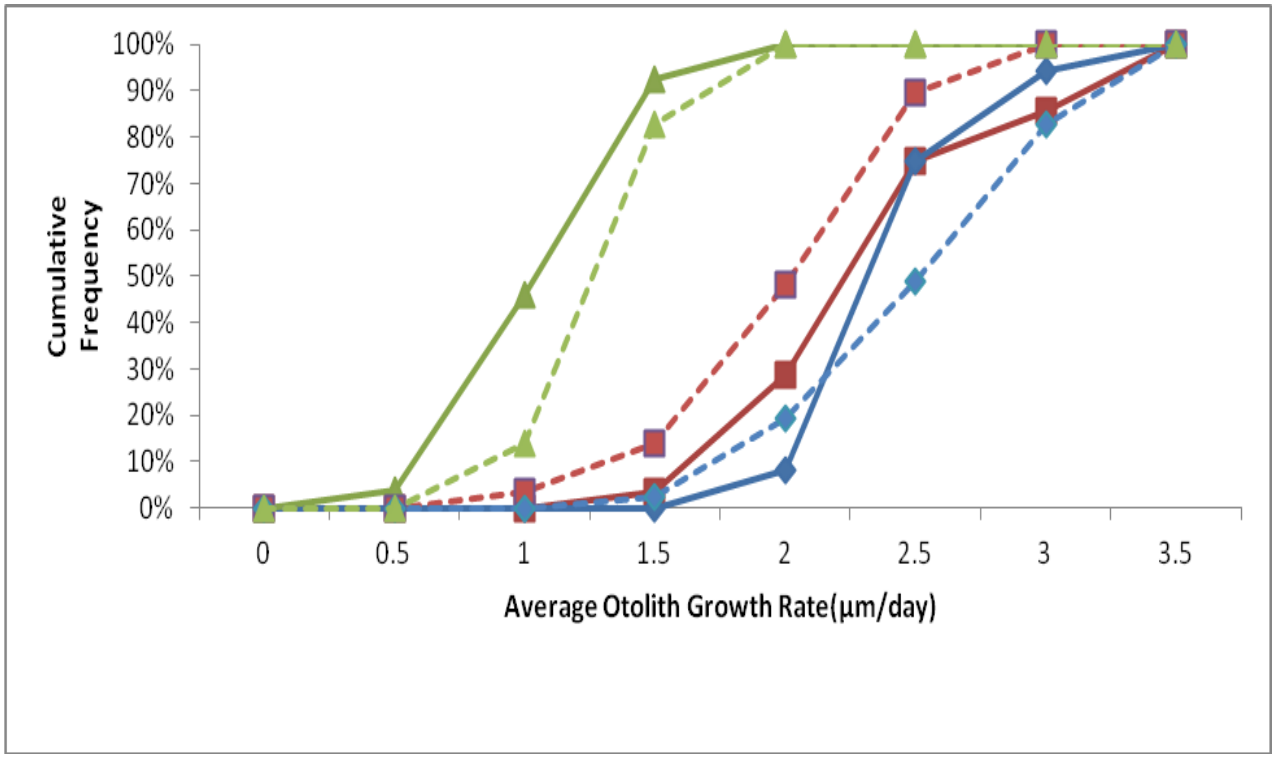

Figure 3. Sensitivity analysis for probabilities of assignment to the Detroit River stock (DR) for juvenile yellow perch in the western basin of Lake Erie during 2006 and 2007. Primary y-axis values indicate the percentage of successful DR assignments (solid lines). Secondary y-axis values indicate the percentage of failed assignments to any site (dotted lines). The x-axis indicates the associated minimum confidence of assignment. Blue lines represent 2006 values, whereas red lines indicate 2007 values.